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Evidence of a Chromosomal Polymorphism Unique to Cercopithecini. A Key Factor in the Tribe Definition ?

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Editorial

There are obvious gaps in the comprehension of genomic mechanisms leading to speciation [1]. This arise the question: "Are genetic differences and polymophism highly responsible in the species isolation mechanisms? Despite many efforts, it might be fundamental collect evidences and bringing more examples in the discussion. Nevertheless, the existence of alternative and incompatible species concepts reflects a basic disagreement about the nature of species. By introducing the biological species concept, Mayr [2] stated that the species is an assemblage of interbreeding natural populations reproductively isolated. Cracraft [3] proposed the phylogenetic species concept affirming that a species is a monophyletic cluster of organisms, a prelude to the ontological concept of Christoffersen [4] that defines the species as the product of a single lineage evolution in a interbreeding history. Species, as concrete biogeographical entity, has a genetic base that limit its essence and protect its existence. Genetic and chromosomal barriers are important in the limitation of fertility and in the arose of varieties and species in animals and plants [5-7]. Conversely, several examples, like Tribe Papionini in Primates, indicate that species differentiation is not necessarily related to genomic differences and/or levels of genetic variability and chromosomal polymorphism. Both variability and polymorphism are highly scrutinized by the natural selection. According to human genetics studies (the largest body of information on genetic variability we have assembled analysing ourselves), humans (HSA) have a level of endured polymorphism in their karyotype. This polymorphism is restricted to the quantitative expression of autosomal heterochromatic traits in pericentromeric areas, or in the expression of NOR's districts, or in the HSA specific Y chromosome q-arm; polymorphism associated to balanced inversions are rare, and umbalanced translocations are strongly selected. Intrinsic genetic mechanisms work well in the protection of species identity.

On the other side, intrinsic genetic barriers are evidently not necessary in potentially interfertile sympatric species, that are reproductively isolated by behavioural mechanisms (sympatric Macaca species with identical genome organization in 42 homologous chomosomes, maintain their reproductive isolation). Even if it is possbile to describe "local" break down in reproductive isolation either in captivity and/or in nature, there is still a open discussion on the (rare) efficacy of hybridization in species creation.

Karyotype assemblage and chromosome features assume a potential importance in speciation. Molecular chromosome studies are certainly a tool in phylogenetic studies [8-10].

If in Papionini (see above discussion) the speciation event is not related to chromosomal changes, and species maintain their isolation, using rigid behavioural schemes, in Cercopithecini, chromosomal rearrangements have played a fundamental role in the birth and separation of populations. Cercopithecus and related species are important models for the study of primate evolution during the Plio-Pleistocene. The group includes genera and species characterised by facial patterns, various ecological distribution, and a vivacious reshuffling of chromosomal features in the different species or in different Species-Group [11]. Some plesiomorphic character like "catamenial swelling" in Allenopithecus or Miopithecus challenge the classical composition of the tribe and indicate a weak phylogenetic relationship of these genera with real guenons. It is known that Cercopithecini Tribe are characterised by a fission-fusion model of chromosomal evolution, and that some synteny disruption occurred in different species with different mechanisms [12]. The intense chromosomal diversity among species has been interpreted as a motif of speciation (reproductive barriers), together with biogeographical clusterization in the African geography.

What if the Cercopithecini in addiction to an highly diploid variation, have a "tribal-specific" chromosomal polymorphism? Cercopithecini tribe is characterised by a HSA20/21 syntenic association [13], an apomorphic trait acquired during the primate evolution. Interestingly, this synteny, constructed by two small human hortologous, can be found in two forms (heteromorphy), in homozygosity or frequently in heterozygosity in different species.

The first description of this chromosomal polymorphism was in occasion of a GTG banding on a *C. nictitans* from the Zoo of Barcelona [14]. Subsequently, a second report was on a *C. nictitans* stampflii from the Zoo of Zurich [15]. This polymorphism was then investigated in other guenons of the same Superspecies group with widely dispersed distribution: *C. mitis maesi* and *C. albogularis labiatus*, animals coming from South African facilities and from the Transvaal forests respectively [16].

On the base of GTG banding this polymorphism was described as a pericentric inversion followed by a paracentric inversion. The pericentric inversion hypothesis seems confirmed by molecular cytogenetics data on other guenons like *C. petaurista* and other species in the Campbelli and Cephus species group (unpublished data), althought a more intriguing hypothesis of a Evolutionary New Centromere (i.e. the activation of centromeric silenced sequences) has been recently proposed by Stanyon et al. [17].

The scrutiny of literature data suggests the presence of the same polymorphis trait even in other Cercopithecoidea related to the genus Cercopithecus [18,19].

The presence of this polymorphism in different species could be a symptom of particular chromosomal dynamics for this syntenic association, and not a result of speciation and genetic drift [20]. Chromosome 21 in humans is a gene poor chromosome with vast areas of duplication and, interestingly, does not contains Fragile Sites. Chromosome 22 is more rich of important genes and has only one rare Fragile Sites in its length. The inversion (or the ENC, if defined in future by molecular approaches), has presumably derived from a common ancestor in Cercopithecoidea. In the hypothesys of an inversion, these mechanisms spread because they prevent recombination from breaking apart sets of alleles that work well in an ecological or sexual setting. Since recombination continues normally within the populations of inverted and uninverted chromosomes, inversions may escape many of the deleterious consequences suffered by other genetic mechanisms that shut down recombination entirely [21]. In many species, including plants, fungi, insects and humans, there is evidence that inversions respond to natural selection; however few genes or other chromosomal features that are the results of selections have been ambigously identified. Thus the mechanisms that affect most of the inversions remains unknown [22].

A part from the molecular mechanism involved in this heteromorphism, our interest is in the phyletic meaning of this peculiarity, in the hypothesis that this polymorphism predate speciation, a very interesting situation that could be symptom of a gene flow and of a phylogenetic and chronologic vicinity within the species in the Tribe. The sporadic but distributed frequency of this polymorphism is unusual and seems the first case of chromosomal polymorphism involving different related-species in a Primates genus and in its sister genera.

Tribe Cercopithecini offers a great variety of interesting parameters that should be carefully interpreted in the light of a multidisciplinary approach and of a re-defined ecological framework to its evolution.

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